CHAPTER 10

Movement ecology of crab plovers in a tidal system: exploring the tide or the tide line?

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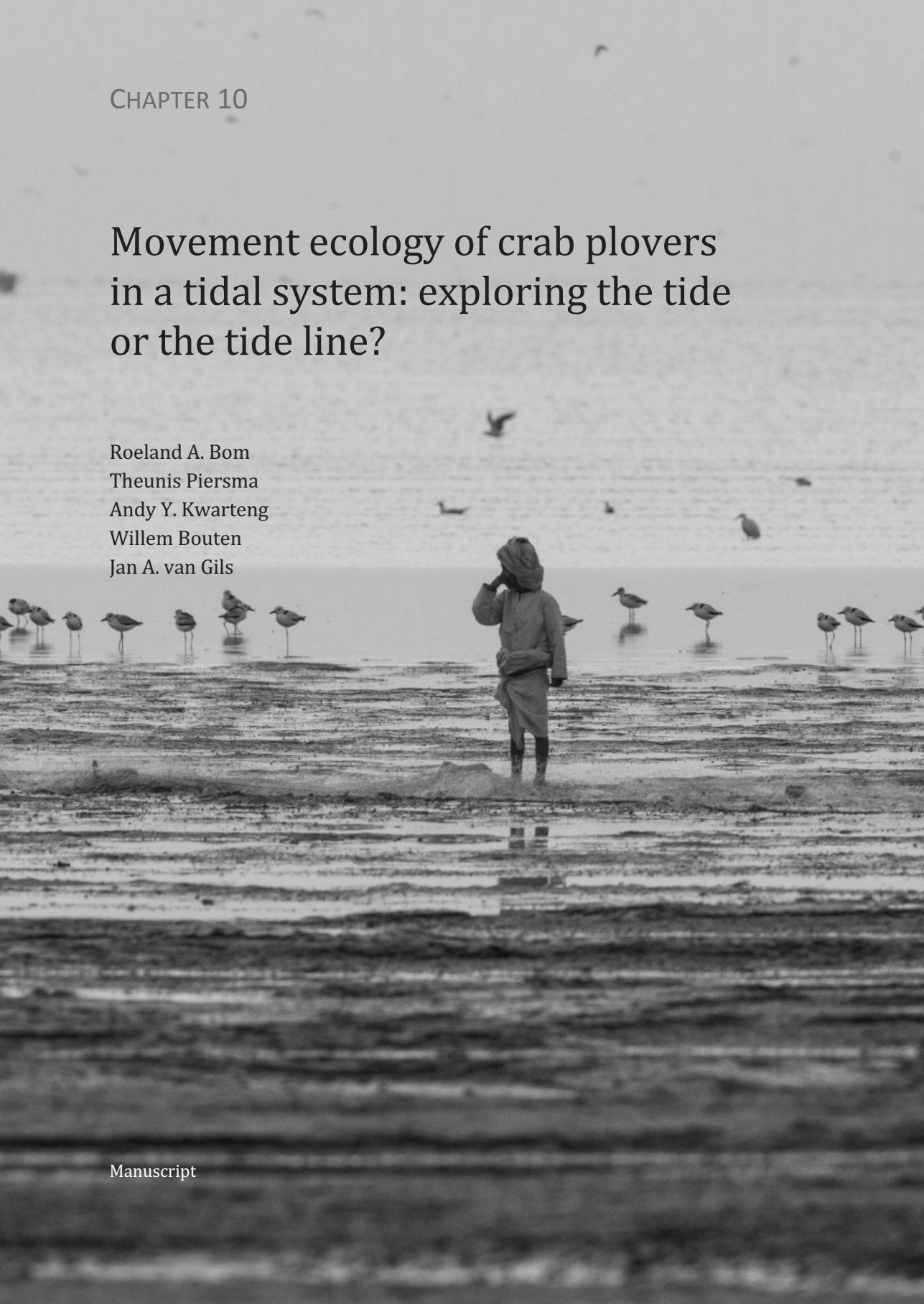

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Abstract

Foragers exploiting intertidal resources face challenges related to the non-alignment of daily and tidal rhythms and with resource availability varying in complex ways. Some avian foragers have been shown to distribute themselves as a function of the extent of the exposed intertidal, whereas other concentrate foraging around the moving tidal edge. Here we study how crab plovers *Dromas ardeola* deal with these tide-specific time and space problems: do they use entire exposed intertidal space or do they follow the tideline? We used GPS- and accelerometer tracking data, obtained on 11 crab plovers in the intertidal of Barr Al Hikman, Sultanate of Oman. Movement patterns cycled in concert with the tidal cycle of 12.4 hours. Birds were away from the roost to actively forage during periods of 8–10 hours centred around low tide. Crab plovers almost always remained close to the water line, presumably because the swimming crabs, their preferred prey, were most active and abundant in and close to the tide line. Birds remained longer at sites where they were shown with accelerometers to handle prey. This suggests that crab plovers exhibit area-restricted search, the expected behaviour for birds foraging on prey showing spatial autocorrelation. Between tides, birds followed the waterline, but with little respect to precise location, as at a grain size of 200 m they hardly revisited sites between consecutive tides. This 'opportunistic' spatial behaviour is expected for birds exploiting resources which are unpredictably distributed, suggesting that swimming crabs move with the waterline but at unpredictable locations. Our study gives an intimate picture of the timing and space use of crab plovers and how they are closely linked with the tide. In this species, most if not all foraging decisions of crab plovers are moulded by a moving waterline.

Introduction

Intertidal areas offer an interesting arena for the study of movement ecology as foraging animals need to solve common time and space problems with intriguing rhythmic features (Bulla *et al.* 2017). To start with, because tidal waters rise twice per lunar day and alternately cover and uncover the intertidal area (de la Iglesia & Johnson 2013), the intertidal resources are unavailable during part of the day (van Gils *et al.* 2006). Because the lunar day last 12.4 hours, the availability changes in time with respect to the circadian rhythm. Thus, animals foraging within the dynamic intertidal areas should schedule their behaviour with the interacting environmental rhythms (Leiva *et al.* 2016; Bulla *et al.* 2017).

In addition to timing-related issues, intertidal foragers should schedule their space use such that they acquire their daily energetic demands. Tidal foragers in search for invertebrate prey items, depending on the prey items they aim to exploit, should concentrate their movements around the moving tide line or extend their movements to exposed or covered mudflats (Both *et al.* 2003; Granadeiro *et al.* 2006). The more sedentary intertidal resources remain hidden under the surface, whereas more mobile prey items are most active in the waterline or move in and out the intertidal area with the tidal flow (Rosa *et al.* 2007; Cardoso *et al.* 2010). On top of that, invertebrate prey are often patchily distributed (Kraan *et al.* 2009). Theory and empirical work shows that foragers exploiting patchily distributed prey items should stay and search longer in the places where resources are abundant and should not spend too much time at sites where there are few resources (Benhamou 1992; Nolet & Mooij 2002; Fryxell *et al.* 2008). In the tidal area the decision to leave a place may also be affected by the incoming or outgoing tide, as over time places become unavailable or places with possible better feeding opportunities become available.

Another movement-related issue is to revisit previously visited areas (Bracis *et al.* 2018). Tidal foragers face this issue multiple times per day, as they are pushed out of the intertidal area with the tidal flow. The degree of animals to return to an area is predicted to decrease as the temporal autocorrelation of resources increases (Switzer 1993; Mueller & Fagan 2008). The temporal predictability of sessile prey such as molluscs and polychaetes may be high between tides, whereas the temporal predictability of mobile resources (e.g. shrimps, crabs and fish) may be lower. But, adding complexity, in tidal areas opportunities to revisit previously visited places are often hampered by the tidal rhythm, as the low tides show different levels because the moon's gravitational pull is added to that of the sun.

Traditionally, visual studies on animals foraging in the intertidal area have been confined to daytime and to relatively small spatial areas (e.g.Zwarts & Esselink 1989) as it is difficult to study animals during the night and when they move out of sight at low tides (but see for instance Hulscher 1976; Piersma *et al.* 1993c). With the onset of GPS and accelerometer tracking technology, it has now become possible to study the space use and the behaviour of individual animals in great detail by day and night, during high and low tide (Shamoun-Baranes *et al.* 2012). Yet, only a few studies have used tracking data to explore how animals schedule their space use and behaviour in complex intertidal systems (van Gils *et al.* 2006; Bijleveld *et al.* 2016; Bulla *et al.* 2017; Dokter *et al.* 2017).

Here we used tracking data to study the spatiotemporal movements and behaviour of crab plovers *Dromas ardeola* foraging on the intertidal mudflats of Barr Al Hikman in the Sultanate of Oman. We amalgamated the challenges that crab plovers face in the dynamic intertidal zone into four questions: (1) when do they forage? (2) do they follow the tide line or do they exploit the mudflats? (3) when do they leave a site? and (4) how often do they revisit previously used sites? Crab plovers are enigmatic shorebirds that breed and winter in tidal areas (De Marchi *et al.* 2015a), primarily foraging on crabs (Rands 1996). In our study area crab plovers forage on mobile swimming crabs or on more sedentary burrow-hiding sentinel crabs (Chapter 8). Weighing about 375 g, crab plovers can carry state-of-the-art GPS- and accelerometer trackers (www.UvA-BiTS.nl; Bouten *et al.* 2013). A previous study (Chapter 9) developed an ethogram of crab plovers based on the classification of accelerometer data.

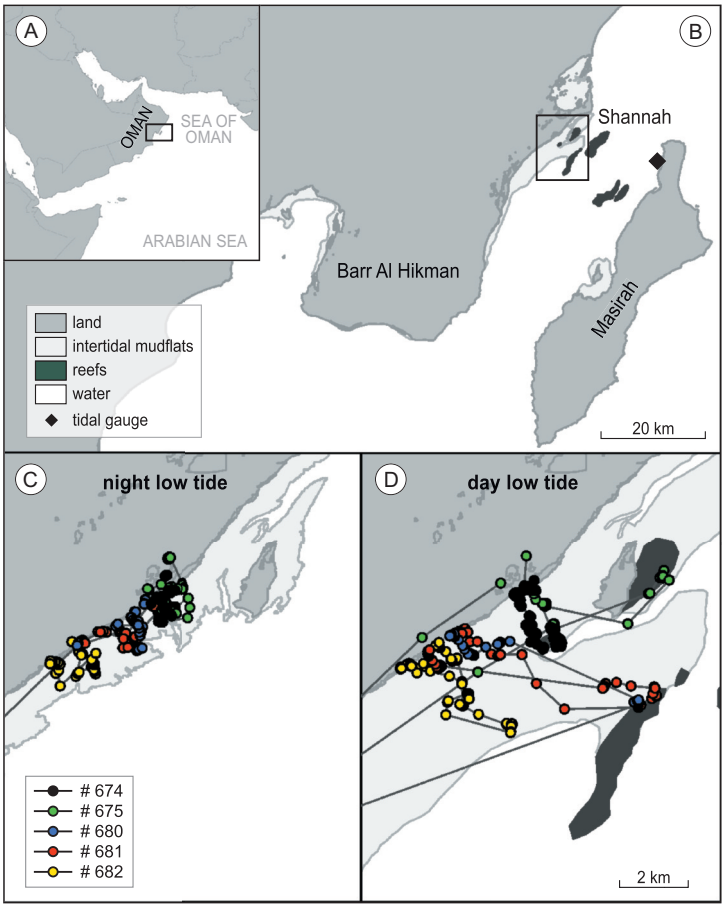


Figure 10.1. (A) The Arabian Peninsula with the location of Barr Al Hikman in the red square. (B) The Barr Al Hikman Peninsula with the intertidal mudflats, reefs and the tidal gauge at Masirah. The red square shows the area depicted in (C) and (D) in which we show (C) the tracking data collected during the first low tide on 1 December 2012, 05:07 with a minimum water level of 1.7 m and in (D) the tracking data collected during the second low tide on 1 December 2012, 17.12 with a minimum water level of 0.7 m.

Methods and Materials

Study system

Barr Al Hikman is a peninsula of approximately 1400 km^2 in the Sultanate of Oman (20.6°N, 58.4°E) (Fig. 10.1A and B). The peninsula is bounded by intertidal mudflats of about 190 km^2. The tidal cycle in the area consists of a mixture of diurnal and semidiurnal tides (Fig. 10.2A, based on a tide gauge at the nearby (25 km) island of Masirah; predicted data from http://www.ukho.gov.uk/Easytide/easytide/, observed data from https://uhslc.soest.hawaii.edu/data/?rq#uh113a). For this study we made observations in the time period 19 November – 31 December 2012 and 18 November – 31 December 2014. Lomb-Scargle periodograms (Lomb, 1985), which determine cycles in time series, showed that for each tide the water level at each second next low tide was more alike than the water level at the next low tide (Fig. 10.2). Furthermore, tides showed recurrent pattern in water level after about 26–32 tides. At a shorter time scale the water level exhibited a clear 12.4 hours and 24 hour rhythm (Fig. 10.2B). The predicted and observed water level at low tide ranged from 0.1 m to 1.9 m (Fig. 10.2A, 10.3A). During the night, defined as the period between sunset and sunrise, the water level of the low tides were significantly higher in the period of observations (Fig. 10.3B, linear model (lm), df = 16, t = 6.820, $P < 0.001$). We confined our observations to the area south-east of Shannah (Fig. 10.1C and 10.1D) in which the size of the exposed intertidal mudflats is related to the water level (Fig. 10.3C, lm, df = 6, t = 12.03, $P < 0.001$, based on a bathymetry map presented in Chapter 3).

Barr Al Hikman is renowned for its abundant birdlife (Chapter 5). For the crab plover, a species that is endemic to the Indo-West Pacific, the area is the most important wintering ground (Chapter 6). About 8,000 individuals can be found in the area between November and March (Chapter 5).

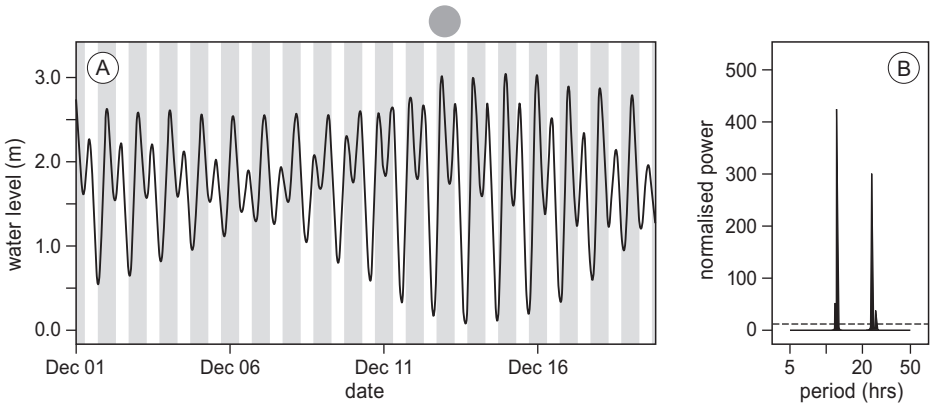


Figure 10.2. (A) Example of the tidal rhythm at Barr Al Hikman for a 18-day period during the study period in 2012. Shaded envelops indicate nights. New moon was on 13 December. Data is based on measured water levels at Hilf, Masirah Island (B) Lomb–Scargle periodogram of the water level shows a distinct peak at 12.4 hours and at 24.0 hours. The dotted horizontal line shows the border above which peaks are considered significant.

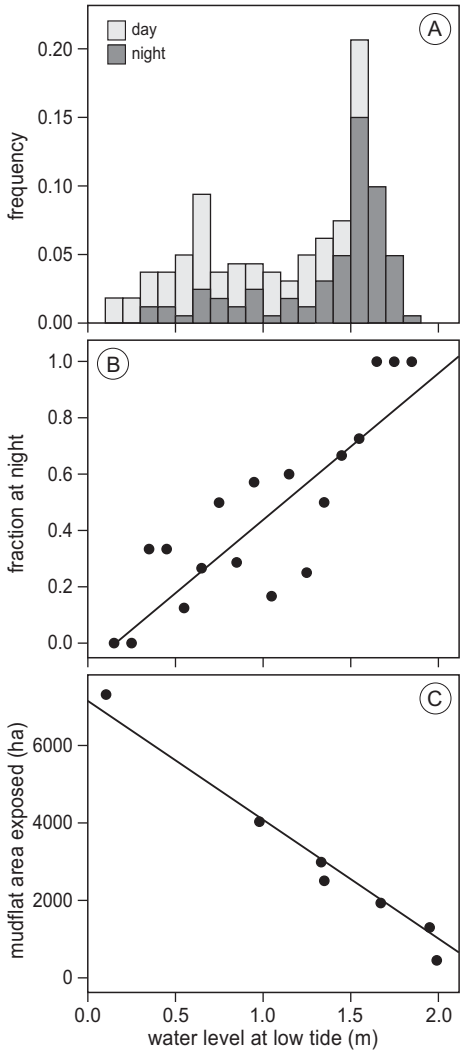


Figure 10.3. (A). Frequency distribution of water level at low tide during the period of observation, with dark bars showing night low tides and light-grey bars showing day low tides. From this figure the fraction of low tides occurring at night was calculated and shown in (B) The water level at low tide is in general higher during the night than during the day. (C). During neapish low tides significantly less mudflats area is exposed . The exposed area was calculated for the east coast of Shannah and based on 6 satellite images.

Tracking details

Crab plovers were caught with mist nets at night. In November 2012 and November 2014 respectively 8 (4 males, 4 females) and 10 (7 males, 3 females) adult crab plovers were fitted with UvA BiTS trackers (Bouten *et al.* 2013) using a full-body harness made of 6 mm wide Teflon strings and weighing about 2 g. In addition, all birds received a unique combination of

colour rings (Chapter 6). Birds were released within 20–40 min after capture. The tracked crab plovers weighed an average of 380 g (SD ± 38 g) in 2012 and 367 (SD ± 41 g) in 2014. The mean weight of the trackers and their attachments was 15.1 g (SD ± 0.5 g) in 2012 and 9.8 gram (SD ± 0.1 g) in 2014. This means that on average the birds had to cope with 3–4 % added mass. In 2012, five of the eight tracked birds stayed within the study area. Two other moved within two days out of the study area to the south of the Barr Al Hikman Peninsula and to Masirah Island. Connection with another bird was lost after a day. In 2014, seven of the 10 birds tracked in 2014 stayed within the study area, of which one stopped working after two days. The number of obtained tracks per tide type per year are given in Table 10.1. All tracked birds that stayed within the study area were regularly observed and behaved as their conspecifics. Crab plover provision their offspring throughout the first winter (De Sanctis *et al.* 2005) and two of the tracked birds in 2014 (#2008 and #2118) were regularly observed feeding a first winter bird. Three of the 8 birds tracked in 2012 were observed in 2013, of which we observed one in 2014. Four of the 10 birds tracked in 2014 were observed in 2015. The area was not visited in 2016. Apparent survival of colour-ringed crab plovers in the area was estimated at 90% (Chapter 6). Four of the seven trackers resighted after a year were still working, but we could not collect enough data to analyse movement details for any individual in more than one year.

The tracking device is solar-powered and includes a GPS receiver and a tri-axial accelerometer which measured acceleration in surge (X), sway (Y) and heave (Z) at 20 Hz. Tracking data is downloaded via a wireless network, which can also be used to upload new sampling schemes. The trackers were set to record position at an interval of 10 minutes. When possible, the trackers were set to sample at a high interval of either 15 or 30 s intervals for about 4 hours around day-time low tide. When battery voltage was low, the trackers stopped recording. Position fixes were always followed by 10 seconds of acceleration measurements.

In crab plovers, acceleration measurements can be usefully transformed into five behaviours: body care, inactive, handle, tactile search, fly and walk (Chapter 9).

Timing of foraging movements

Non-foraging crab plovers aggregate on roosts, usually around high tide, were they remain mostly inactive (Chapter 6). Thus, to study how crab plovers schedule their timing of foraging

Table 10.1. Number of tides at which tracks were obtained from each tracked birds, the number of 'complete' tracks collected (defined as a track at which more than 90% of the 10 minute interval measurements were collected) and the number of tides during which high resolution measurements were obtained.

	2012					2014					
	#674	#675	#680	#681	#682	#2008	#2114	#2116	#2117	#2118	#2119
# of tides tracked	80	58	49	79	78	35	21	26	41	44	55
# of 'complete' tides	38	23	29	33	43	32	15	22	30	42	43
# of tides with high resolution data	26	27	20	25	20	8	9	11	10	19	22
# of tides between first and last tide	79	74	70	79	79	35	23	24	53	44	55

movement we analysed periodic patterns of distance to the roost and the amount of active behaviour using the Lomb-Scargle or least-squares periodogram method. The Lomb-Scargle method is an alternative to traditional Fourier analysis and is ideal for analysing tracking data as it can be used on unevenly sampled data (Péron *et al.* 2016). The roost was defined as any position on the mainland. The amount of active behaviour was defined as the percentage time spent on all behaviours except no-motion and body care, as measured with the acceleration based ethograms (Chapter 9). For computational convenience a dataset was created on a 10-minute interval. For tides in which higher resolution data was collected we created 10-minutes data by making bouts of 10 minutes in which we calculated the median position and the average percentage of all behaviour.

We found that the foraging movement of crab plovers followed a tidal as well as a circadian rhythm. In the night birds stayed closer to their roost and were less active. As the water level is in general higher during the night (see above) we studied if the foraging movements in the night were a result of the day-night cycle or of the water level. To this end we selected for each bird and per low-tide water level an equal number of day and night tides. Day tides where defined as tides with a low-tide time more than 2.5 hours prior to sunset or 2.5 hours after sunrise and a similar approach was used to define night times. Confining measurement to 2.5 hours around low tide, we calculated for each selected tide and per bird the average distance to the roost and the time spent inactive. We then compared whether any of these factors differed between day and night using linear mixed-effect models with individual as a random effect. All analyses were done using the R software (R Development Core Team 2013). Distance to roost was calculated using the *gDistance* function in the *rgeos* package, Lomb-Scargle periodograms using the *lsp* function in the *lomb* package and mixed-effect models using the *lme* function in the *nlme* package.

Following the waterline or exploring the exposed intertidal mudflats?

To study whether crab plovers followed the water line or explored the mudflats we calculated the distance to the waterline for each position. This was done by first extracting for each measurement the tidal height at that specific moment from the tide measurements at Masirah. As tidal measurements were available at an hourly basis we interpolated the tidal height using the *ftide* function in *TideHarmonics* package in the R software. We then calculated the position of water line, based on the bathymetry map available for the area (Chapter 3). This was possible because the bathymetry map gives a measure of elevation relative to the waterline. In our approach the waterline is given as a defined position of the waterline, whereas in reality the transition between exposed and flooded mudflats is not so stringent, especially with the ebbing tide. The calculations were done on the 10-minute interval data. Besides that we calculated the distance to the water for the real positions, we additionally calculated the distance to the water for a simulated bird exploring the mudflats, i.e. for each measured position we simulated a random location on mudflats that were exposed at that moment. We calculated the distance to the waterline using the *gDistance* function in the *rgeos* package in the R software. Negative distances indicates positions in the water and positive distances positions on exposed mudflats. As the bathymetry map did not cover the reefs found in the low tidal zone we excluded all locations on reefs.

Patch use

We studied if bird stayed longer at a place, further referred to as a patch, when successful. A patch was defined by the foraging animal's behavior (c.f. Kacelnik & Bernstein 1988); if a bird travelled more than 200 m in 10 min we assumed that it entered a new patch. Birds were assumed to be successful if they were found handling, indicated by the acceleration data. To exclude the possibility that birds stayed longer in a patch because it was handling, patch-residence time was calculated as the time spent in a patch minus the time spent handling in that patch. Because acceleration data was obtained for about 33% of the time, the exact total handling time in a patch could not be directly calculated. Therefore, we estimated the total time spent handling in a patch as the average time handling multiplied by the total residence time. We also checked if birds spent more time inactive in 'handling patches', for instance to digest food.

Furthermore we studied if the decision to leave a patch was related to a decrease in handling time (i.e. foraging success) and to the water level. For this latter analysis we divided each patch visit into two halves of equal duration and then calculated if birds handled more in the first part. We used the R package *recursive* to define patches and to calculate patch-residence time. Calculations of patch use were based on the high-resolution data (Table 10.1). To make sure that we included positions of foraging birds only we excluded all positions less than 200 m away from the roosts and positions where birds were flying. For the statistical analysis we calculated per bird the mean patch residence time for 'handling patches' and 'no-handling patches'. To explore possible cues that underlie the decision to leave a patch we analysed the relationship between patch-residence time and handling probability and the relationship between time spent inactive and handling probability with linear mixed models, using the R package *nlme*. Likewise we analysed if the distance to the waterline at patch departure differed between 'handling patches' and 'no handling patches', making a distinction between the ebbing tide and the flooding tide. Bird id was entered as random effect. Visual inspection of the residual plots revealed no deviations from normality.

Revisit rate

To study if birds revisit places in subsequent tides we calculated for each bird a revisit rate against the tidal time lag. For each tidal time lag x the revisit rate was calculated as the number of revisited places on tide $t + x$ divided by the number of visited places on tide t (hence a value of 1 would mean that all sites were revisited and a value of zero no revisits). To this end we used the *getRecursions* function in the R package *recursive* (Bracis *et al.* 2018). We used a circle with a radius of 200 m moving along the trajectory with 10-minute data. At each point, the number of trajectory segments entering and exiting the circle was counted to determine the number of revisits (Bracis *et al.* 2018). The studied spatial scale of 200 m matches with the scale at which we sampled the prey of the crab plover (Chapter 3). Smaller and larger radius (100 m to 1000 m) gave qualitatively similar results. Positions less than 200 m away from the roosts and positions where birds were flying were excluded. Only itineraries in which the tracker was on for more than 90% of the time were included (Table 10.1). To explore possible causes of individual differences in revisit rate we relate for each individual its mean revisit rate for the first 23 tides (the maximum time lag for bird #2114) to the mean distance travelled per

tide (calculated as the sum of the distances between each point) using linear models. Likewise we related for each individual the mean revisit rate to the average time handling per tide (as a measure of absolute foraging success) and to the average time handling divided by the average time searching and walking (as a measure of relative foraging success) using linear models. Furthermore we tested if there was a difference in revisit rate between birds that were found provisioning and birds that were not seen provisioning (referred to as independent) using a one-way ANOVA.

Results

Timing of foraging movements

Lomb-Scargle periodograms showed a clear peak at 12.4 hours and 24 hours in the distance to the roost and active behaviour (Table 10.2). This means that crab plovers exhibit both a tidal and circadian foraging rhythm. Actograms (Fig. 10.4A and Appendix A10.1) and ethograms (Fig. 10.4B and Appendix A10.1) showed that the 12.4 peak is related to the tidal height, with birds going further from the roost (Fig. 10.5 and Appendix A10.2) and being less active around low tide. In the night, birds were closer to the roost and were less active than during the day (Fig. 10.4). In the subset of data in which we tested if the tendency to stay closer at the roost was related to the day-night cycle or to the water level we found no difference in distance to roost ($t = -1.007048$, $df = 10$, $P = 0.34$), and in activity $t = -1.49654$, $df = 10$, $P = 0.14$), suggesting that the differences in the day-night cycle are exclusively related to the tidal cycle, rather than to the light-dark cycle.

Table 10.2. Frequency values of the first and second peak measured with Lomb-Scargle periodograms. Values give medians and interquartile range calculated over estimates per individual.

	first peak (hrs)	**second peak** (hrs)
distance to roost	12.40 (12.38 – 12.44)	23.99 (23.91 – 24.07)
active behaviour	12.43 (12.41 – 12.45)	23.99 (23.90 – 24.08)

Following the waterline or exploring the mudflats?

Although there was considerable variation between individuals and between tides (Appendix A10.3), in general crab plovers stayed close to the waterline rather than exploiting the entire tidal flats at low tide (Fig. 10.5). With the outgoing tide birds lagged behind the waterline and with the incoming tide, around two hours after low tide, the water line took over the birds (Fig. 10.5).

Patch use

Birds stayed longer at patches where acceleration data showed that it has been handling ($t = 15.904790$, $df = 10$, $P = 0$, Fig. 10.6). The tendency of birds to stay longer at 'handling patches'

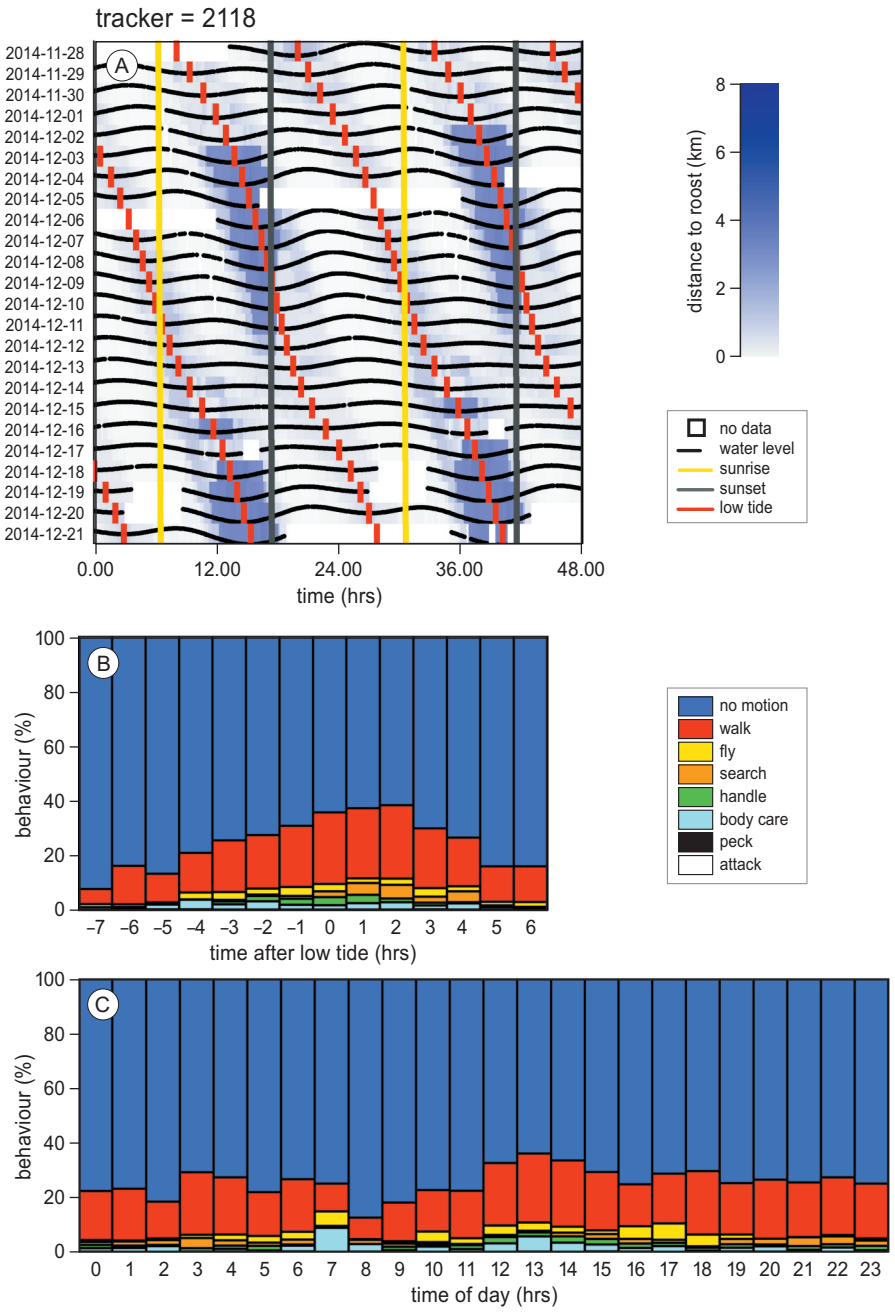


Figure 10.4. (A) Example of the actogram showing the distance to the roost over time (the darker the blue the further away) for the bird with tracker #2118. Note that between 2 and 11 December when the bird moved closer to the roost around sunset (timing of sunset given by dark-grey line). Ethograms showing the different behaviours of the same crab plover in relation to the time after low tide (B) and the time of the day (C). The data was pooled for all tides and hours respectively. See the actograms and ethograms for all studied birds in Appendix A10.1.

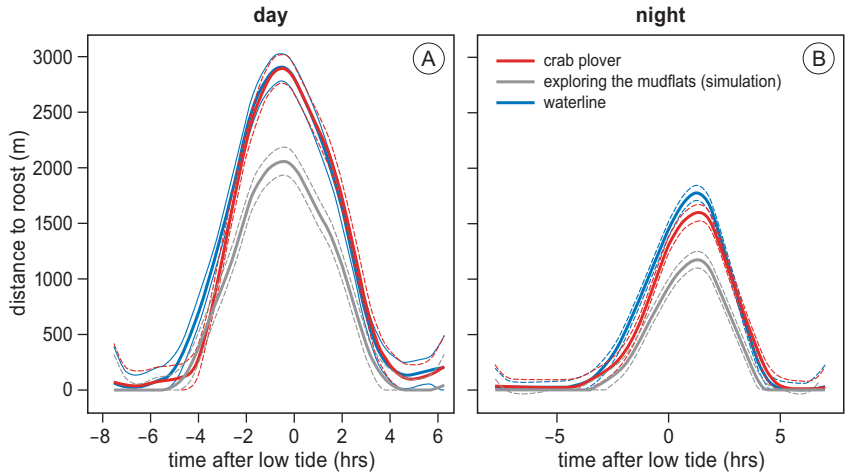


Figure 10.5. Summary of the movements of crab plovers in relation to the tidal cycle during (A) day and (B) night. The red lines show the distance to roost in relation to the time after low tide. The blue lines show the average distance to the waterline added to that of the distance to the roost, thus showing that birds before low tide move slightly behind the waterline and after low tide birds spent on average more time in the water. The grey line show a simulation of a bird randomly exploring the exposed mudflats. Solid lines are average lines interpolated with a loess smoother, dotted lines show 95% confidence intervals showing variation between individuals. See Appendix A10.2 & A10.3 for graphs on distance to the roost and distance to the waterline for individual birds.

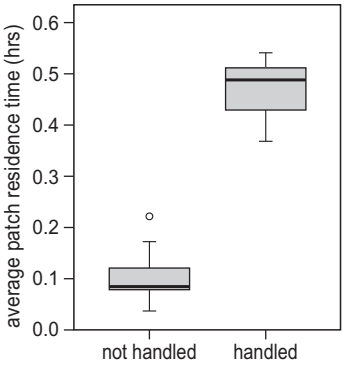


Figure 10.6. Average patch residence time on patches where birds did not and did handle prey items (according to acceleration data). Residence time was calculated by excluding the time spent handling so, the tendency to stay longer at a patch was not because of the time spent handling. Boxplots show variation in individual averages.

was not because birds spent more time inactive as there was no difference in the percentage of time inactive between 'handling patches' and 'no-handling patches' ($t = -0.94974$, $df = 10$, $P = 0.3646$). The average time spent handling was equally long in the first half within a patch compared to the second half ($t = -0.2129012$, $df = 10$, $P = 0.2052$). At the patch departure time, the distance to the waterline did not differ between 'handling patches' and 'no handling patches' neither at the ebbing tide, nor at the flooding tide ($t = 0.1646353$, $df = 30$, $P = 0.87$).

Revisit rate

In general the tracked birds revisited less than 20% of the places (Fig. 10.7A). The revisit rate decreased with increasing time lag between tides and approached 0 after around 50 tides. For the first 10 tides the revisit rate showed a clear zigzag pattern in relation to the time lag, meaning that the revisit rate was a higher at each second-next tide (Fig. 10.7A), which coincides with the mixed semi-diurnal tidal pattern (Fig. 10.2). In addition, the revisit rate showed a peak after about 30 tides, which coincide with the recurrent pattern in water level (Fig. 10.2). There was no relation between mean revisit rate and mean distance travelled per tide ($F = 1.118$, $df = 1$, $P = 0.3180$), the average time spent handling per tide ($F = 2.668$, $df = 1$, $P = 0.1368$) and the relative foraging success per tide ($F = 2.068$, $df = 1$, $P = 0.1843$). The two birds that were observed provisioning a juvenile bird had a significant higher revisit rate than independent birds (Fig. 10.7B, $F = 9.606$, $df = 1$, $p = 0.0127$).

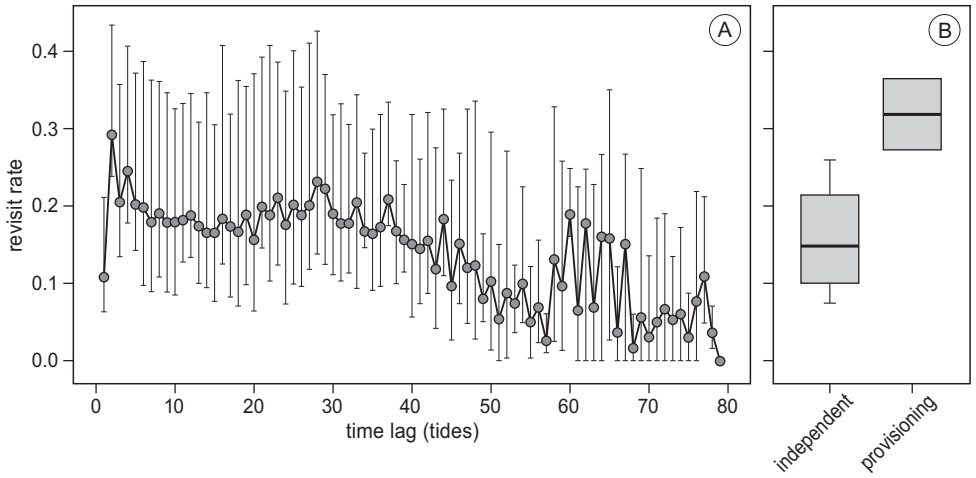


Figure 10.7. (A) Revisit rate as a function of time lag. Red points show the mean revisit rate calculated over individual mean. Error bars show 95% confidence intervals. The number of individuals included for each time lag can be obtained from Table 10.2. (B) Variation in revisit rate for birds that were observed to be independent and that were seen provisioning a first-winter bird. Boxplot show variation in mean individual revisit rate calculated over the first 23 tides.

Discussion

Our tracking data showed that all movements and behaviour of crab plovers within Barr Al Hikman was tightly structured by the tidal rhythm of 12.4 hours. As expected, crab plovers stayed close to the roost and remained inactive around high tide. During periods of 8-10 hours around low tide, crab plovers moved away from their roost and were actively foraging. Less expected, but clearly shown by our data, is that in addition to the tidal rhythm crab plovers exhibited a circadian rhythm of 24 hours, as birds stayed closer to the roost and were less

active at night. Yet, the water level in the night tides are in general higher (Fig. 10.2A and 10.3B) and the analysis in which we compared day and night tides with similar water levels showed no differences in activity or distance to roost. This indicates that also the nocturnal movements of crab plovers are closely linked to the tidal cycle, rather than to the dark-light cycle.

Although the general conclusion is that movements of crab plovers are closely linked to the tidal cycle, it was obvious from the actograms that at some occasions the tracked birds strongly reacted to the nightfall when they moved closer to the roost. Inspection of the data shows that this movement was often from the reefs to the mudflats, suggesting that feeding opportunities interact with place and day and night. Furthermore, the behaviour of the tracked birds correlated with sunrise, when birds showed a peak in body care and flying (Fig. 10.4C and Appendix A10.1). The peak in flying, we assume, is a response to avian predators, notably marsh harriers *Circus aeruginosus*, which are mainly active at that time period.

Crab plovers almost always stayed close to the water line (Fig. 10.5). This indicates that they preferably foraged on prey that is active at or close to the waterline, as is the case in several other shorebirds (Both *et al.* 2003; Granadeiro *et al.* 2006; Piersma *et al.* 2017). Detailed observations on crab plovers in Barr Al Hikman, in a confined area up to 2 km from the coasts (i.e. roost), shows that crab plovers primarily forage on swimming crabs, and to a lesser extent on burrowing crabs, fish and shrimps (Chapter 8). Outside this area crab plovers could not be studied visually, but the tracking data suggests that crab plovers continued foraging on swimming crabs, fish and shrimps (and not on burrowing crabs), as these are the species that are active in or close to the waterline on occur throughout the entire tidal zone (Chapter 2, 3).

Accelerometer data indicated that birds, while following the waterline, stayed longer at 'patches' in which prey items were found (Fig. 10.6). In these 'handling patches' birds remained active, so the tendency to stay longer was not because of prey digestion. This suggests that crab plovers continued searching for prey at places where they have been successful: a behaviour known as area-restricted search (Smith 1974; Benhamou 1992). Area-restricted search has been documented before in shorebirds foraging in a tidal landscape (Dias *et al.* 2009; van Gils *et al.* 2015), and is beneficial for a forager when prey densities are spatially autocorrelated, which is found in many tidal resources (Kraan *et al.* 2009). Indeed, also swimming crabs, the preferred prey of crab plovers, show some degree of autocorrelation, but this differs between years (Appendix A10.2).

Our tracking data did not reveal the nitty-gritty details of what determines a crab plover to leave a patch. The time spent handling in a patch was equally long in the first half of the patch compared to the last half, suggesting that the decision to leave a patch was not because birds were less successful over time. We also did not find that birds left the 'handling patches' later with respect to the ingoing or outgoing tide, suggesting that the water level was also not the cue to leave a patch. Further research, perhaps a combination of tracking data and visual observations, is required to better understand what affects the decision to leave a patch.

While following the waterline, crab plovers did this rather 'opportunistically' as birds hardly revisited locations between consecutive tides (Fig. 10.7A). Theory predicts that the tendency of animals to revisit sites should increase as the temporal predictability of resource distributions increases (Switzer 1993; Mueller & Fagan 2008), and several tracking studies are

in line with this prediction (Weimerskirch 2007; Fryxell *et al.* 2008). Also the 'opportunistic' behaviour of crab plovers may well be a result of an unpredictable food source, as swimming crabs tidally move with the waterline and therefore, between tides, the spatial predictability may be low (Chapter 3 and 8). Yet, there may be some temporal predictability in the prey, as birds tended to revisit sites more often in tides with a similar low-tide water level, indicated by (1) the zig-zag pattern in revisit rate (and matching with the mixed semi-diurnal tide, Fig. 10.2A) and (2) the tendency to revisit sites more often after about 30 tides (matching the lunar-driven recursive tidal pattern at Barr Al Hikman, Fig. 10.2A). Finally, we cannot exclude that the 'opportunistic' behaviour of the crab plovers is a result of food depletion, caused by crab plovers. However, given that the prey is active in the waterline and may well redistribute with every tide, we do not consider this a likely possibility.

The tendency to return to previously visited sites differed considerable between individuals (Fig. 10.7A). These differences likely reflect variation in the individual itself rather than variation in the environment because the studied crab plovers moved in the same area. Yet, for now we have little knowledge on the nature of individuality in crab plovers, and the number of tracked birds restrict extensive analysis at the individual level. Interestingly however, the two birds that were observed provisioning a first winter bird had the highest revisit rate of all birds (Fig. 10.7B). This was not a consequence of restricted mobility, which is sometimes found in animals that accompany their offspring (van Beest *et al.* 2011), as the total length travelled per tide did not show a relation with revisit rate. We speculate that the benefits of returning to the same area may be found in not losing each other.

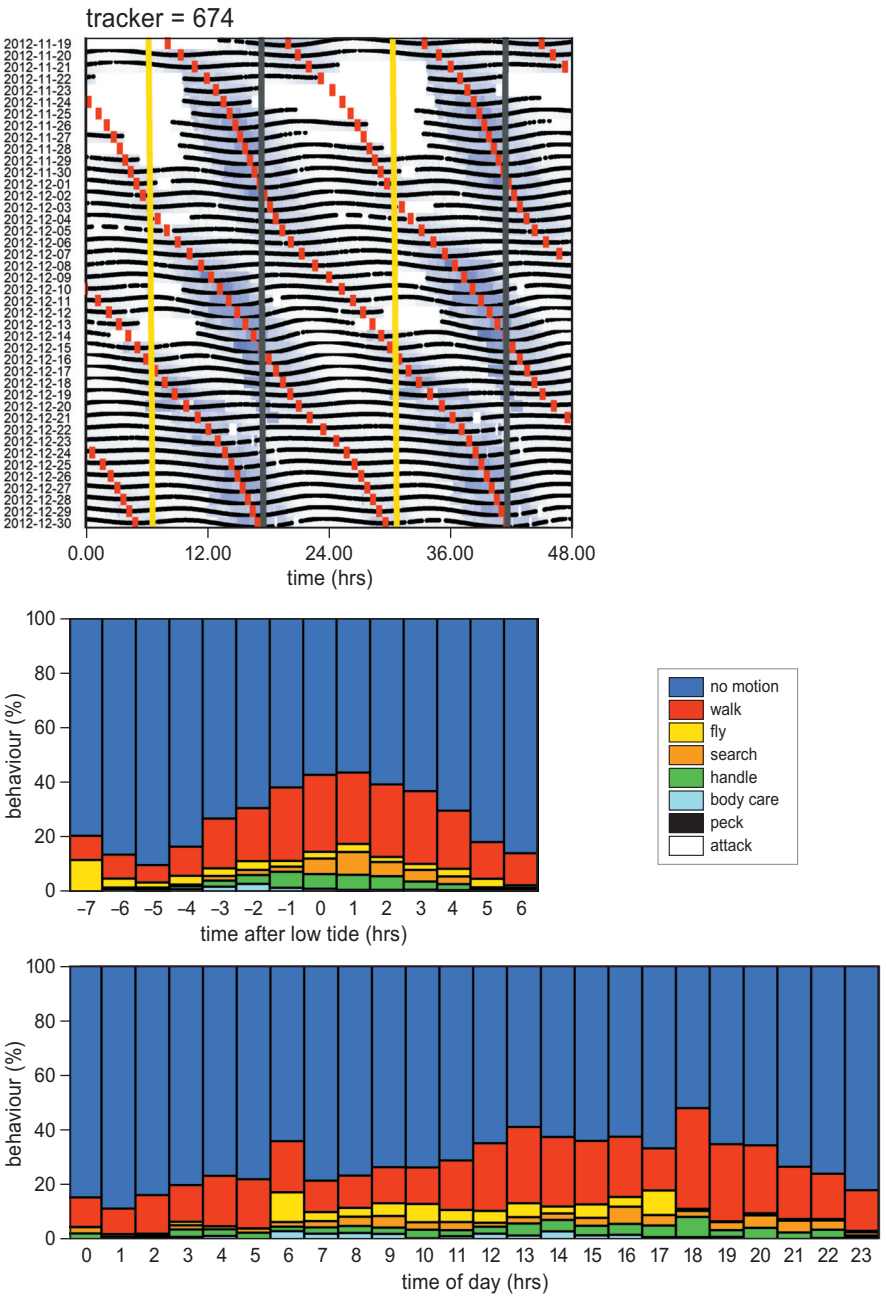
Finally, we acknowledge that we did not consider interactions with conspecifics or predators, whereas both are well known to affect space use in shorebirds (Both *et al.* 2003; Folmer & Piersma 2012; van den Hout *et al.* 2014). Indeed, the peak in flying behaviour in the sunrise hours, presumably in response to marsh harriers, shows that it is not only foraging that matters in the lives of crab plovers wintering at Barr Al Hikman. Furthermore, although crab plovers do not forage in closely aggregated groups, they do forage loosely together, and so a decision to stay or move may also be influenced by the foraging success of conspecifics (such as in red knots, Bijleveld *et al.* 2015b). Although all such factors may affect foraging decisions, we believe that with the current study we have taken a big step in unravelling the mechanisms that drive behaviour and space use of crab plovers, which may contribute to better understand of the movement ecology of tidally foraging shorebirds in general.

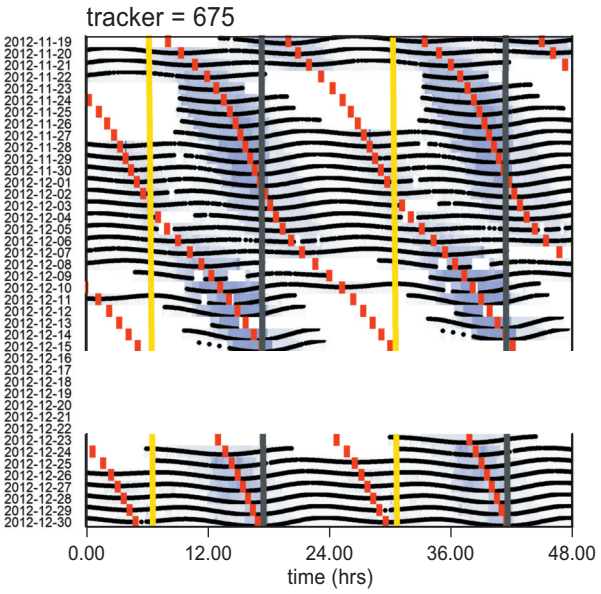
Acknowledgements

Many volunteers helped with catching and tracking of crab plovers. We especially thank Kees Oosterbeek and Symen Deuzeman for exciting times in the field. We thank Allert Bijleveld, Martin Bulla and Thomas Oudman for inspiring discussions. Our study was financially supported by the Research Council (TRC) of the Sultanate of Oman (ORG/EBR/12/002 grant awarded to AYK) and by NWO in the Netherlands (ALW Open Programme grant 821.01.001 awarded to JAvG). Catching, tagging and banding of crab plovers was carried out under permission of the Ministry of Environment and Climate Affairs, Sultanate of Oman. We are grateful to the assistant Director-General Ms. Thuraya Said Al-Sairiri and Director-General Mr Sulieman Al Akhzami for their assistance.

Appendix A10

A10.1 Actograms and ethograms for all tracked birds except for #2118 which was shown in the manuscript

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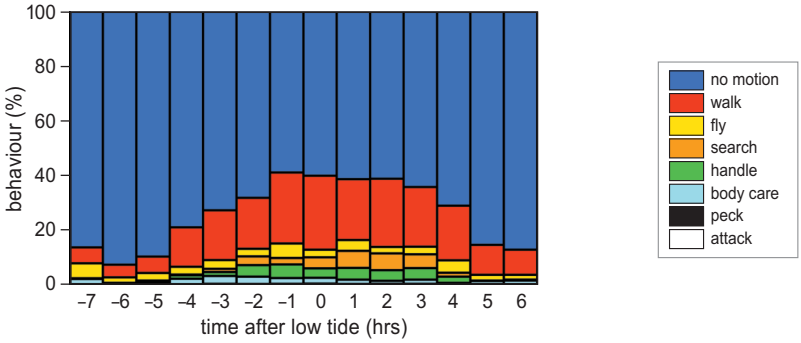
36.00
48.00
time (hrs)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60
40
20
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time after low tide (hrs)
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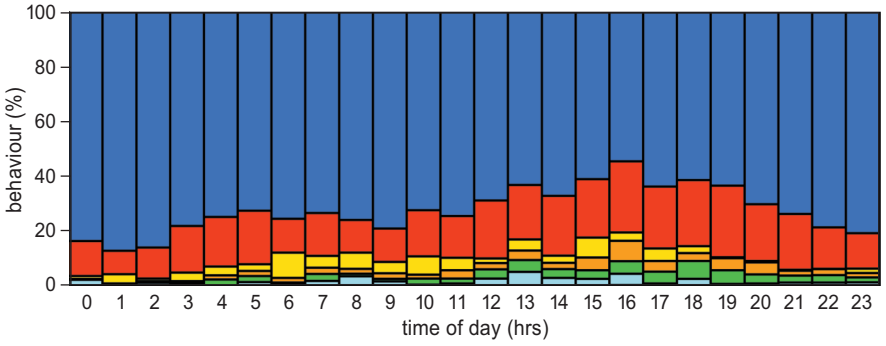
fly
search
handle
body care
peck
attack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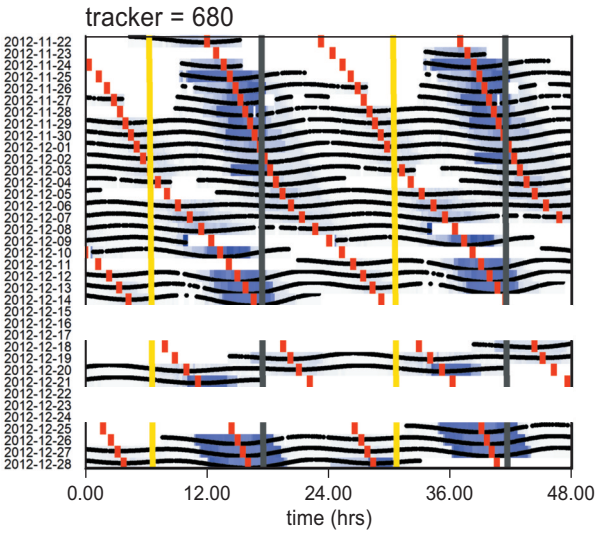
time of day (hrs)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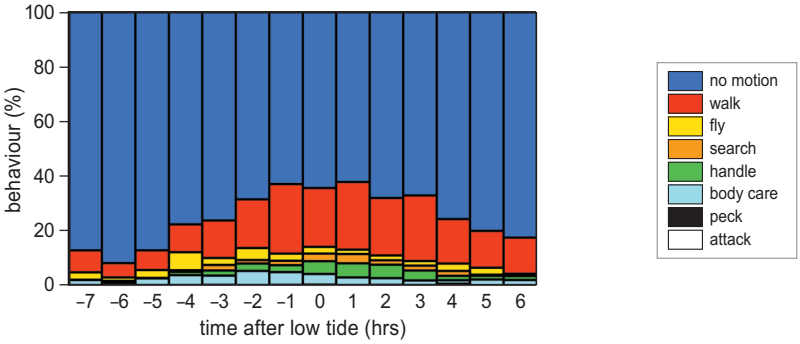
time (hrs)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time after low tide (hrs)
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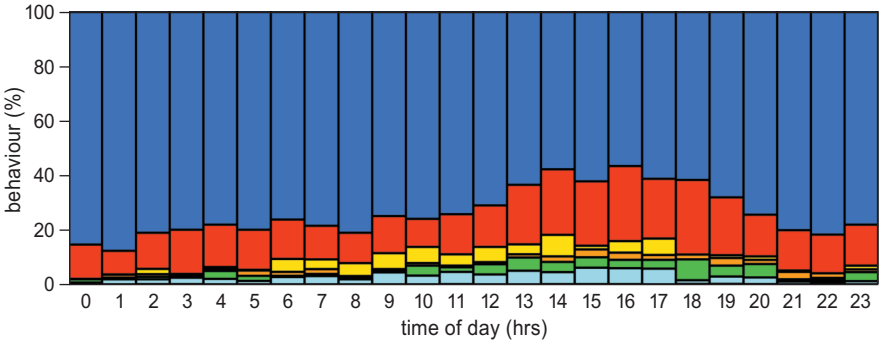
walk
fly
search
handle
body care
peck
attack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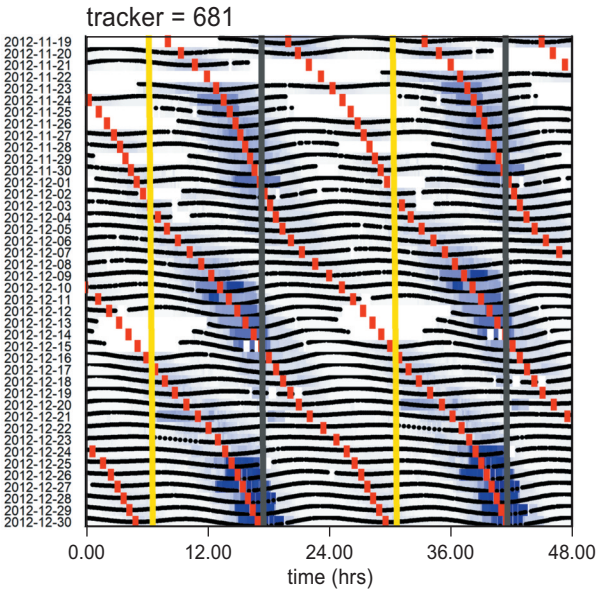
time of day (hrs)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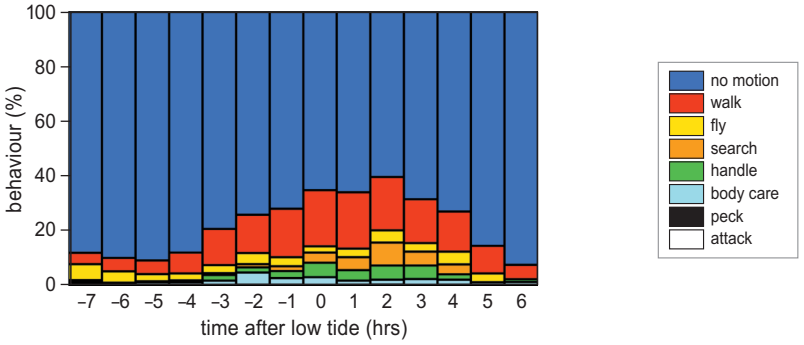
time (hrs)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time after low tide (hrs)
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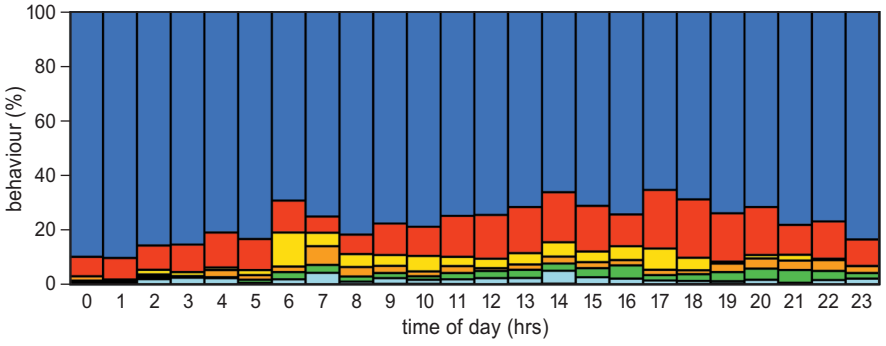
fly
search
handle
body care
peck
attack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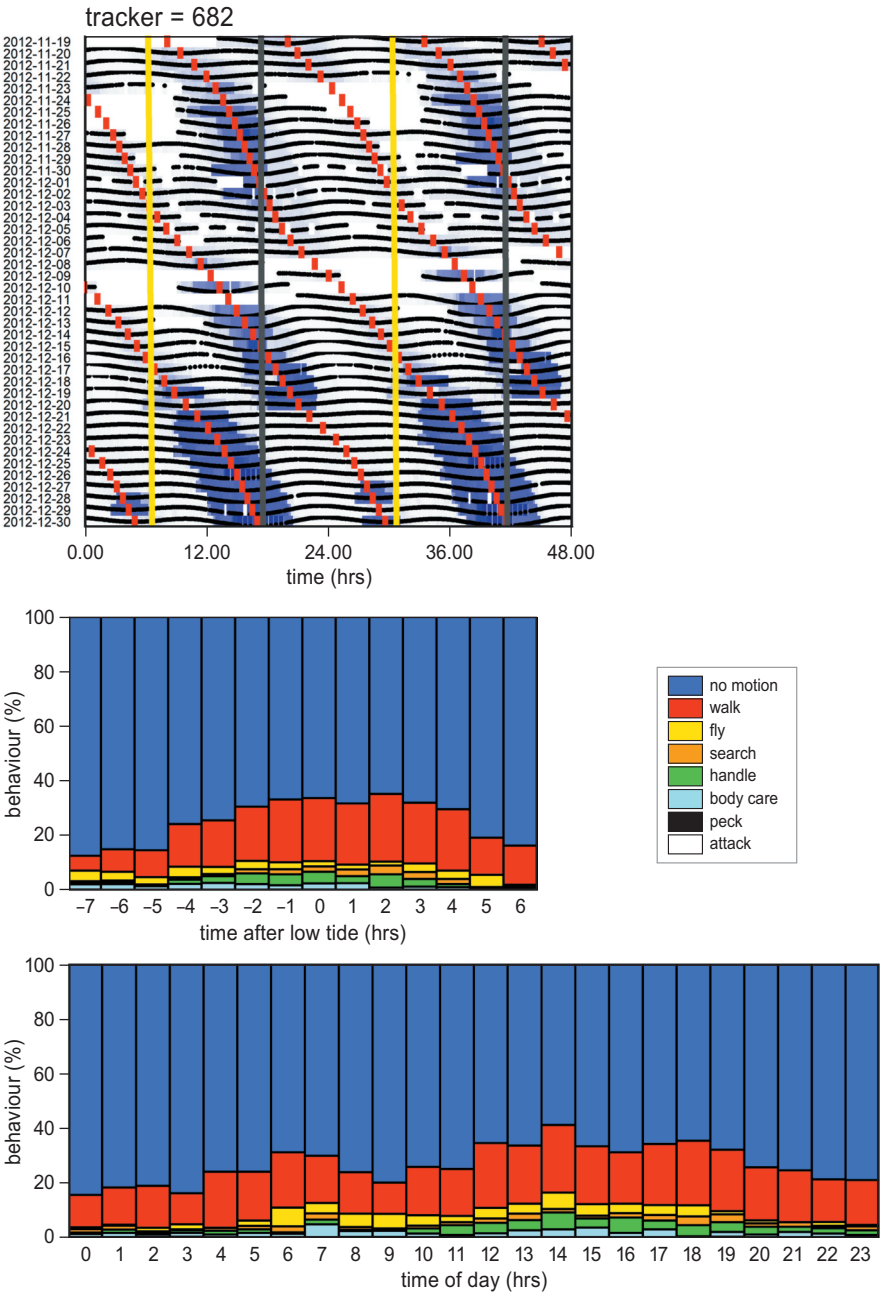
time of day (hrs)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24.00
36.00
48.00
time (hrs)
behaviour (%)
100
80
60
40
20
0
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time after low tide (hrs)
no motion
walk
fly
search
handle
body care
peck
attack
behaviour (%)
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60
40
20
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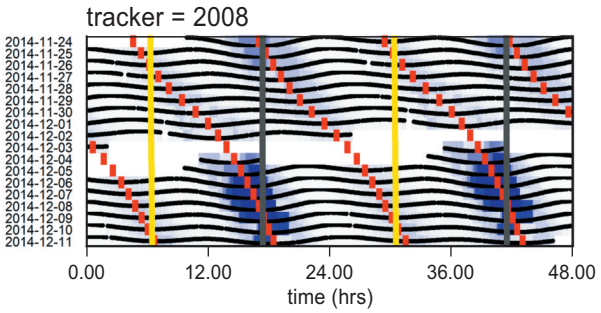
time of day (hrs)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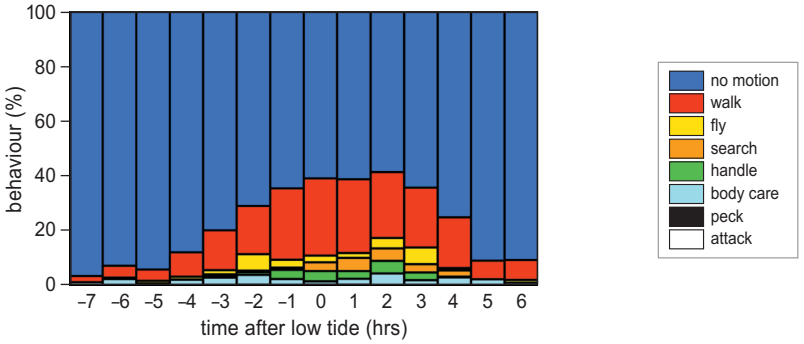
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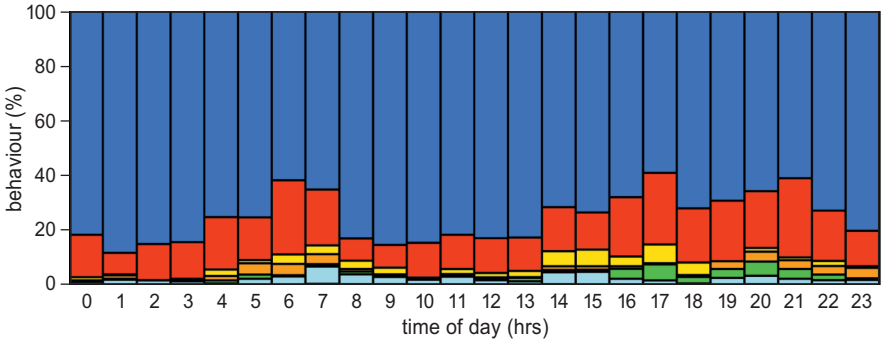
peck
attack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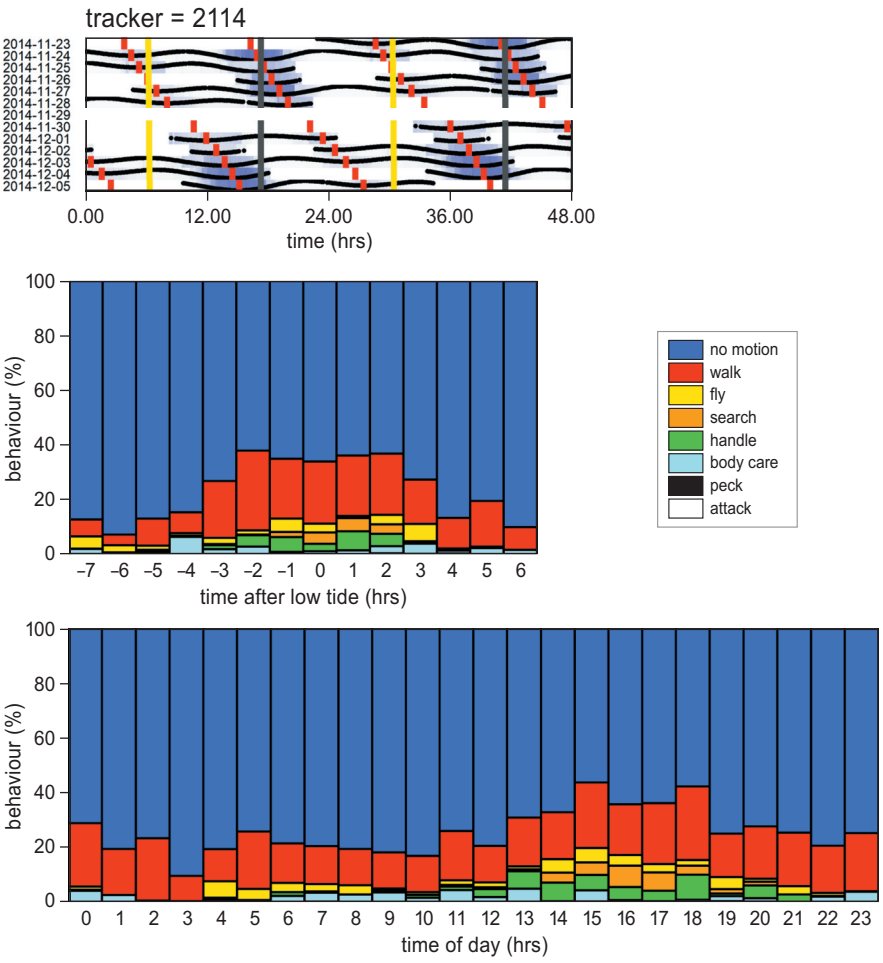
time of day (hrs)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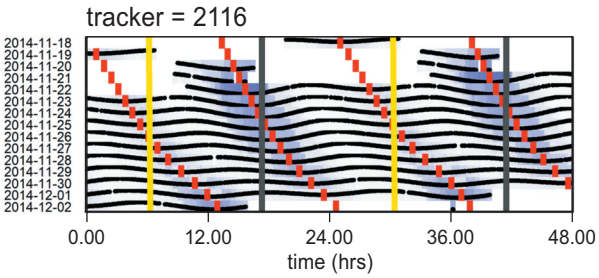
0.00
12.00
24.00
36.00
48.00
time (hrs)
behaviour (%)
time after low tide (hrs)
no motion
walk
fly
search
handle
body care
peck
attack
time of day (hrs)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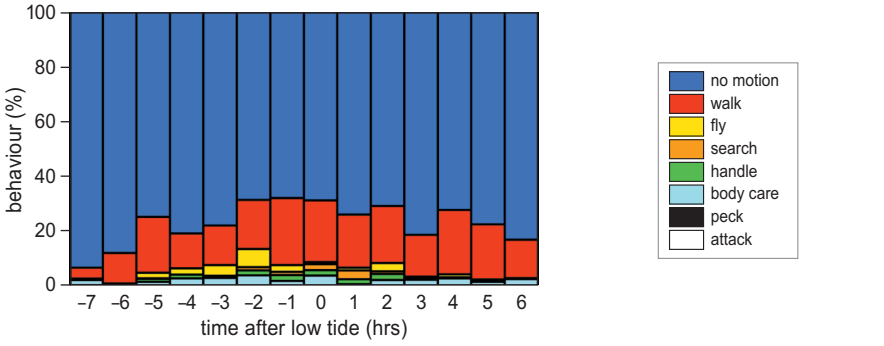
time (hrs)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time after low tide (hrs)
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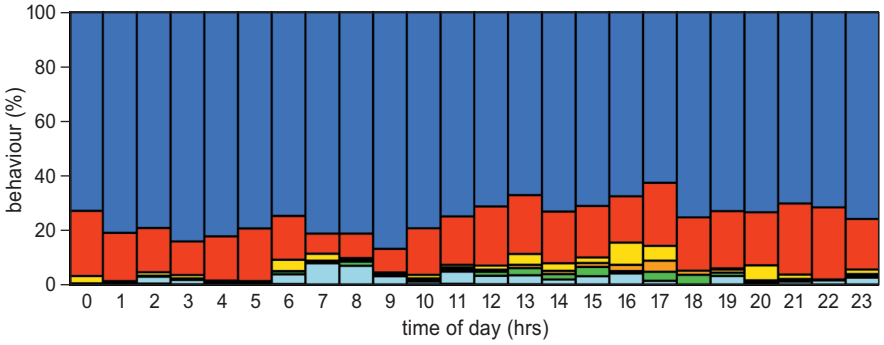
handle
body care
peck
attack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60
80
100
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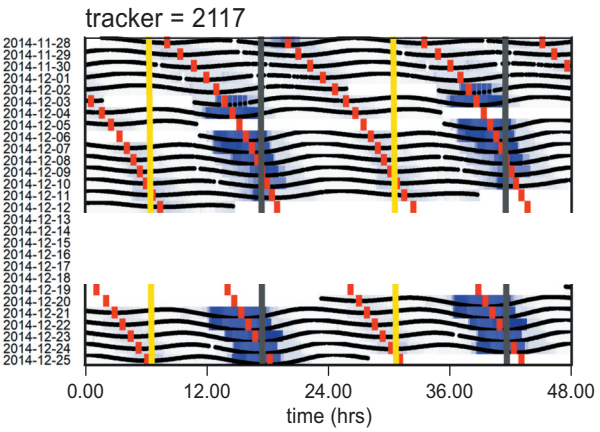
time of day (hrs)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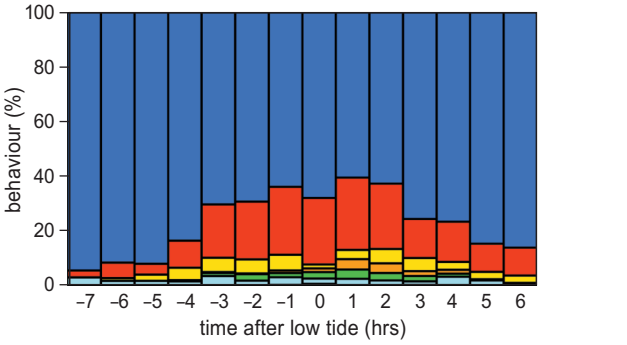
time (hrs)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time after low tide (hrs)
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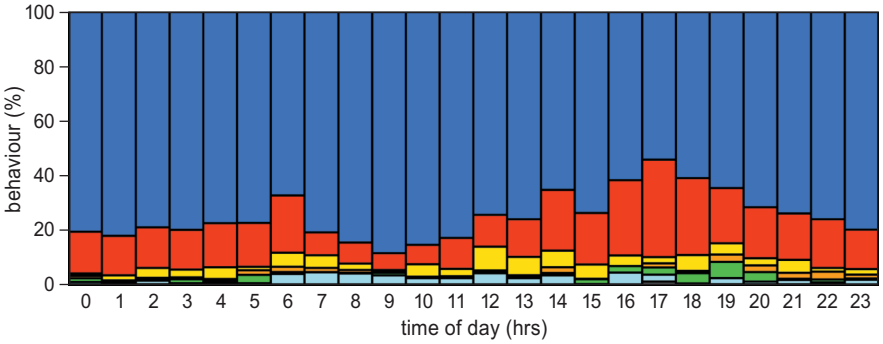
search
handle
body care
peck
attack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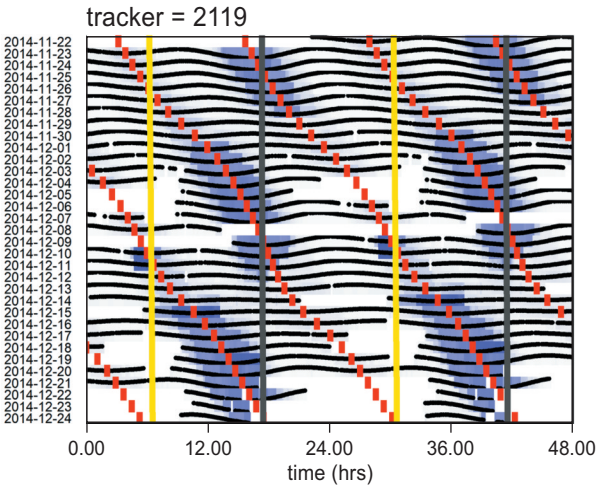
time of day (hrs)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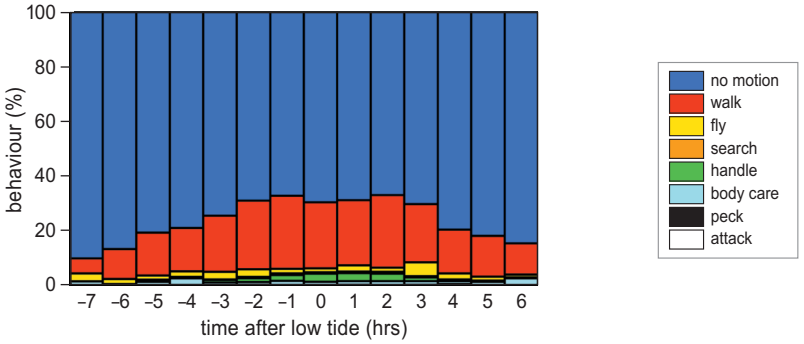
time (hrs)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time after low tide (hrs)
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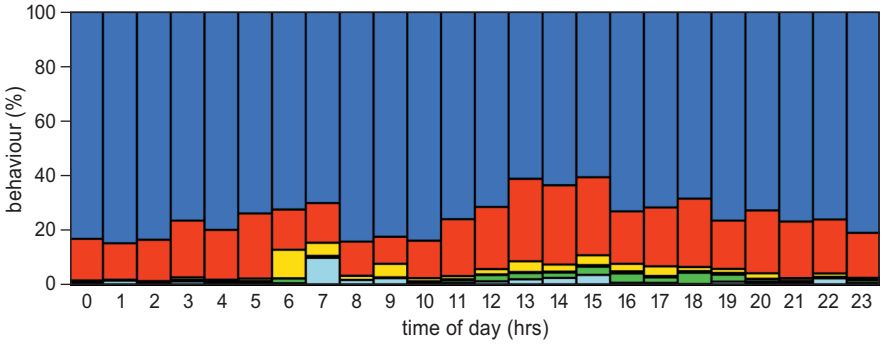
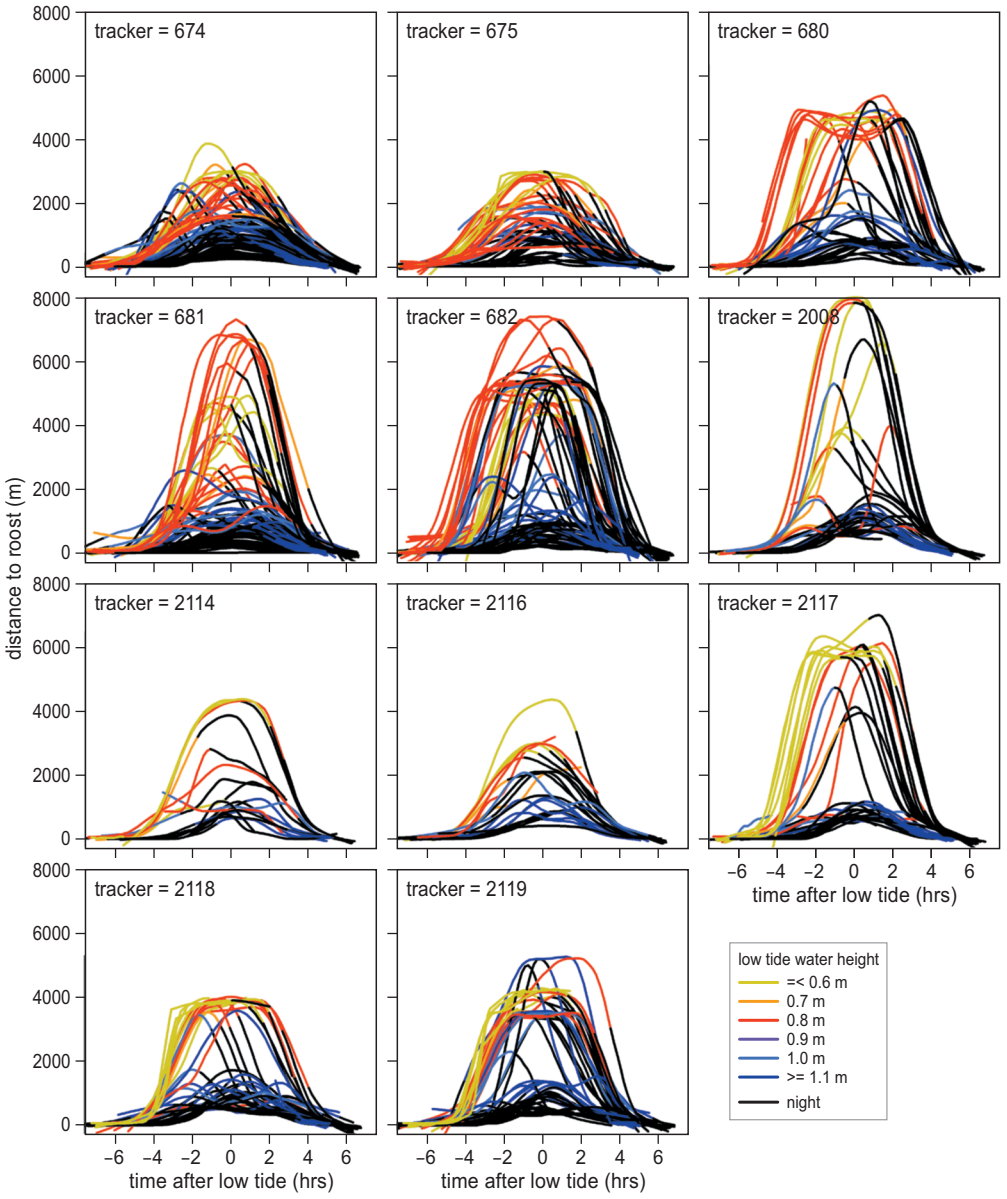
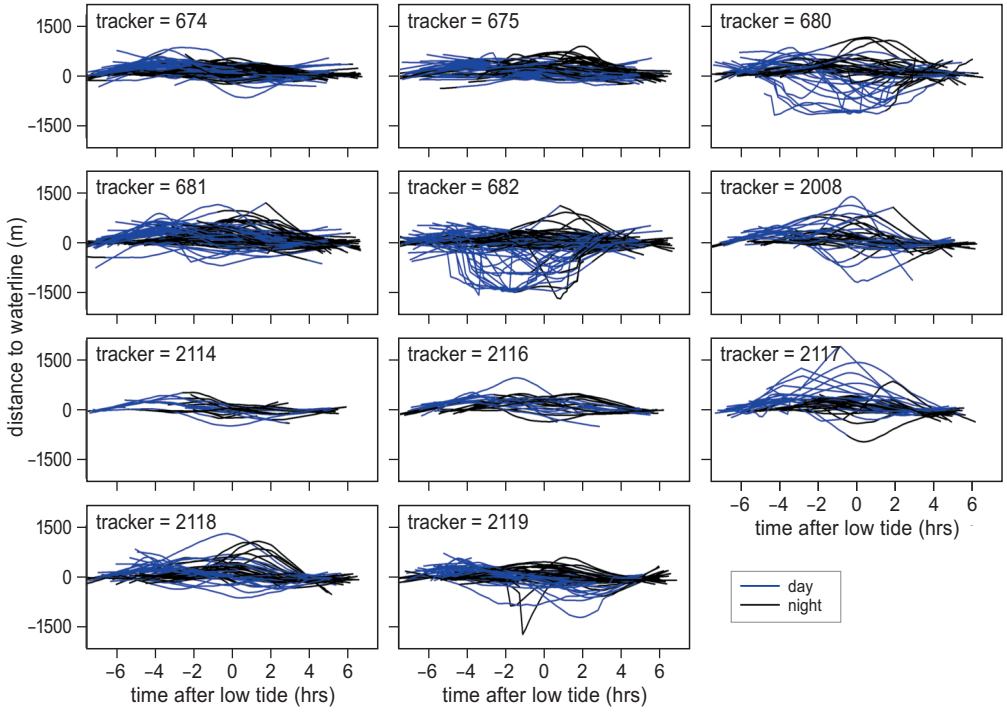
walk
fly
search
handle
body care
peck
attack

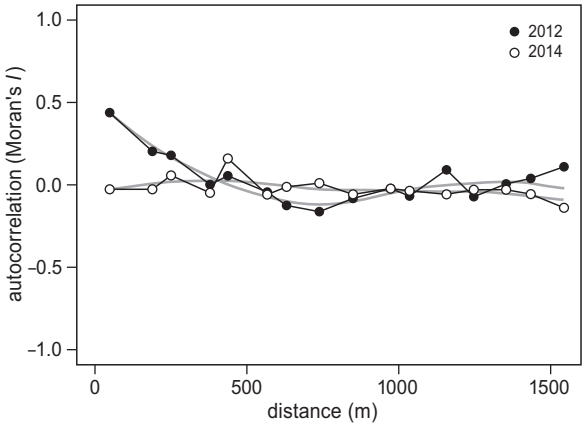

behaviour (%)
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
time of day (hrs)



Appendix A10.2. Individual variation in the distance to the roost in relation to the time to low tide, for all tracked tides. Lines are interpolated with a loess smoother.



Appendix A10.3. Individual variation in the distance to the waterline in relation to the time to low tide, for all tracked tides. Lines are interpolated with a loess smoother.



Appendix A10.4. Correlogram of numerical swimming crab density in the two years of tracking. Spatial autocorrelation was estimated by calculating Moran's *I* values, based on samples collected at a spatial grid of 200 m, plus additional random points (for details see Chapter 3). Because samples were collected over multiple days we cannot exclude that temporal factors affect the obtained spatial correlation. Yet, at short distances samples were taken on the same day and likely the obtained autocorrelation at distances smaller than 500 m reflects spatial autocorrelation only.

Box B

Migration of crab plovers wintering at Barr Al Hikman

Most crab plovers leave Barr Al Hikman in spring (Eriksen & Victor 2013). The migration and the breeding areas of crab plovers wintering at Barr Al Hikman was previously unknown. We obtained seven migration tracks from six GPS-tracked birds (see Chapter 9 and 10 for tracking details). All birds migrated to breeding areas in the extreme north-west corner of the Arabian/Persian Gulf. Three birds spent the summer at known breeding areas at Dara Island in the very south-west coast of Iran (Tayefeh *et al.* 2011). Three other birds spent the summer at breeding areas in Kuwait (Chapter 11), situated at less than 50 km distance from Dara Island. Six birds ringed at Barr Al Hikman were observed in the same breeding area in the same summer. Together, these two breeding areas host about one-third of the world population of crab plovers (Chapter 11). The local movements of the tracked birds in the breeding areas never concentrated around a single place for more than four weeks, suggesting that none of the tracking birds had a succesful breeding attempt. This may have been a conseqence of the tag, which is situated on the back of the bird and perhaps negatively affects the freedom of movement inside the burrow.

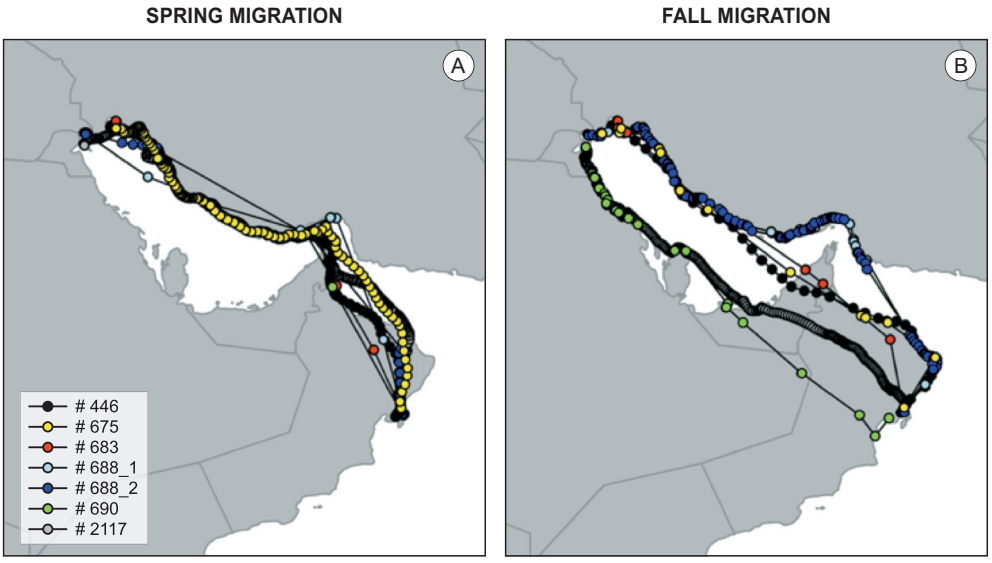


Figure B.1. (A) Spring migration routes of six tracked birds. (B) Fall migration routes for the same birds. Two full migrations were obtained from bird with tracker #688.

All tracked birds took a rather similar route during spring migration. After departing from Barr Al Hikman they migrated straight north, crossing the desert of the Wahiba Sands (Oman) and the Jebel Akhdar mountains (Oman) (Fig. B.1A). The highest recorded altitude was 1495 m, while flying over the mountains. After reaching the north coast of Oman, the birds closely followed the coastline of the Arabian/Persian Gulf further north and west until arrival al the breeding areas in Kuwait and Iran. Because the sampling interval differed between individuals (ranging from 10 minutes to 0.5 days), we cannot compare the distance travelled. The bird with the tracker having the smallest sampling interval, 10 minutes, travelled 2087 km on spring migration, which should be regarded as the minumum distance this bird travelled.

The route during fall migration was more variable among individuals. Four birds migrated along the northern coasts of the Arabian/Persian Gulf. Two other birds followed the southern coasts instead. These latter two birds crossed the empty quarter (the vast desert covering the border area of Saudi Arabia and Oman), flying for about 600 km over the desert. This latter behaviour is in line with one rare observation of a group of crab plovers flying over the middle of the Omani dessert (Mike Jennings pers. comm).

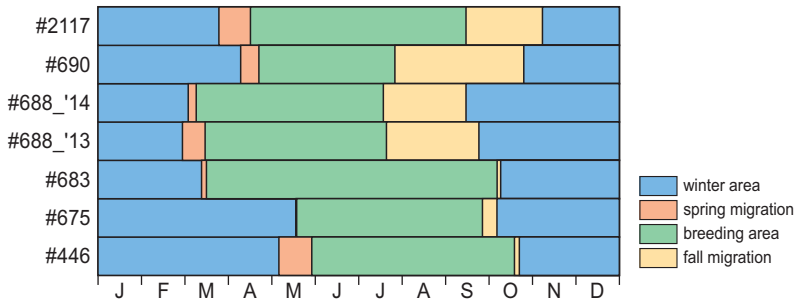


Figure B.2. Annual cycle of six tracked crab plover that winter at Barr al Hikman. Spring migration was defined as the period between departure from Barr Al Hikman and arrival at the breeding areas. Likewise, fall migration was defined as the period between departure from the breeding areas and arrival at Barr Al Hikman.

All tracked birds had several stopovers along the migration route. They usually departed in the early evening and migrated during the night until the early morning and then stopped. Presumably, they did this to avoid flying in the heat. Some birds showed longer stopover periods on both spring and fall migration. The number of days between departure from Barr Al Hikman and arrival at the breeding areas ranged between 3 and 24 days (Fig. B.2). The fall migration took between 3 and 91 days. In spring, the departure date at Barr Al Hikman was related to the arrival date at the breeding grounds, suggesting that crab plovers do not compensate for a late spring departure (Fig. B.3A). In fall there was no relation between the date of departure at the breeding areas and date of arrival at Barr Al Hikman. Early departing birds arrived in the wintering area around the same week as late departing birds (Fig. B.3B).

One bird was tracked for two subsequent years. The migration route of this bird was consistent in the two years, and the timing of the major phenological events were within the same week (Fig. B.1 & B.2 & B.3).

This study is the second to report migration tracks of crab plovers. Earlier, one crab plover was deployed with a tracker at its breeding area in the United Arab Emirates. It migrated to Aldabra on the Seychelle islands (also see Chapter 5) (Javed *et al.* 2011).

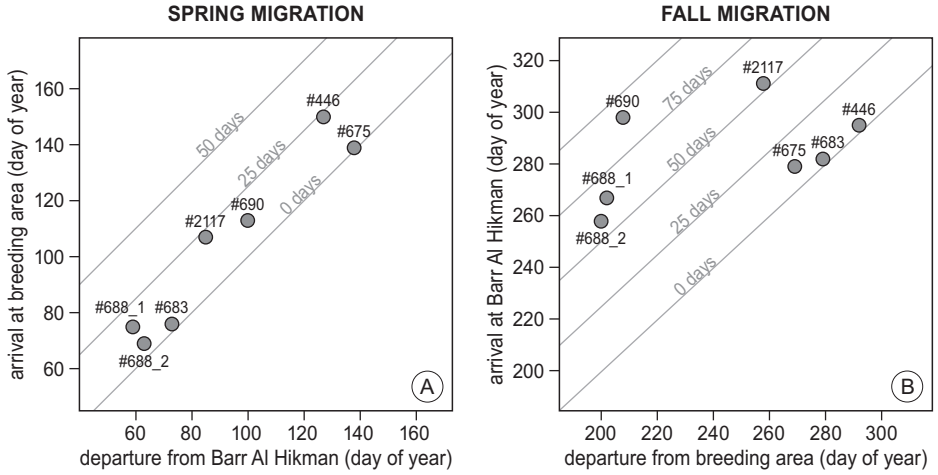


Figure B.3. (A) Spring migration. The day of arrival at the breeding areas is plotted against the day of departure from Barr Al Hikman. (B) Fall migration. The day of arrival at Barr Al Hikman is plotted against the departure day at the breeding areas. Numbers in the circles refer to the tracker IDs.